



Plate II. — Fig. 1. *Giraffa camelopardalis* dext. Coll. Zool. Museum, Amsterdam (No. 964). A = medial view; B = distal view. — Fig. 2. *Antilope cervicapra* sin. Coll. Geol. Inst. Utrecht. A = distal view; B = dorsal view. — Fig. 3. *Cervus cretensis* sin. Coll. Geol. Inst. Utrecht, dorsal view. a = navico-cuboid; b = cuneiforme II/II; c = cuneiforme I; d = anterior facet for the cannon bone; e = posterior facet for the cannon bone; f = tendon leading to musculus peroneus longus; g = tendon leading to musculus tibialis.

The explanation or consequence of the fusion in the tarsus can be sought in a stiffening of the joint, this will restrict the lateral movement and goes together with more flexibility in anterior-posterior direction.

Conclusions

Concluding we may say that besides the general known fusions of bones, others occur which must have had also a functional meaning. One of the described fusions is that of the navico-cuboid and the metatarsals in the island ruminants.

We see that such specialized runners evolve their foot structure (fusions and shortening of the metapodials and phalanges) if circumstances change (islands and lack of predators) and that this new structure will be similarly developed independently from geography and time. It is found so far in the bovids of the pleistocene of Mallorca and in the cervids of the miocene of Gargano and in the pleistocene of Crete and Malta.

The fusion of the magnum and trapezoid in *Parahippus blackbergi* is another case. This fusion occurs in an evolutionary stage in the horse phylogeny in which the function of the lateral digits become reduced and the locomotion apparatus changed essentially. The fusion of these two bones seems a good solution in shifting the weight from the second to the third metapodial. However, this solution was not continued in later horses. Perhaps in other characters this horse was less successful. On the other hand in ruminantia the similar fusion of magnum and trapezoid has become a stable character of the whole group.

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Summary

Some uncommon fusions in tarsals and carpals in Perissodactyla and Artiodactyla are described and the functional meaning of those fusions is discussed. In the described fusions two kinds of origins are distinguished. One kind evolves in ruminants under certain ecological conditions (those are not bound to geography nor to time) and the other occurs in a certain evolutionary stage of a group which is time-geographically-bound.

Zusammenfassung

Funktionelle Verwachsungen von Fußknochen bei Ungulaten

Einige ungewöhnliche Verwachsungen von Tarsal- und Carpalknochen bei Perissodactyla und Artiodactyla werden beschrieben, und die funktionelle Deutung dieser Verwachsungen wird diskutiert.

Die beschriebenen Verwachsungen kann man sich wie folgt entstanden denken: Eine Art entsteht bei den Ruminantia unter bestimmten ökologischen Bedingungen, die nicht geographisch oder zeitlich gebunden sind. Die andere Art kommt in einer Phase der Evolution einer Gruppe vor, die sowohl geographisch als auch zeitlich gebunden ist.

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Courtship behaviour of the wild goat

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Introduction

The wild goat, known scientifically either as *Capra bircus* or *C. aegagrus* (see ELLERMAN, MORRISON-SCOTT 1951; HARRISON 1968) is found on several Greek islands, in parts of Turkey, Iraq, Iran and Afghanistan, in the Caucasus and Turkmenia areas of Russia, and in the Baluchistan and Sind provinces of Pakistan. Because the wild goat of Pakistan supposedly lacks prominent knobs on the horns, and is said to be smaller in size, and have a paler coat than the animals farther west, it has been given the subspecific name *blythi* (LYDEKKER 1900). However, as STOCKLEY (1928) and ROBERTS (1967) have pointed out, the two subspecies (*aegagrus* and *blythi*) of wild goat are so similar in appearance that taxonomic distinctions may be unjustified. Published observations on the behavior of the wild goat consist of natural history notes (DANFORD 1875; WAHBY 1931; ROBERTS 1967) and hunting accounts (STOCKLEY 1928; MAYDON 1937). To add to the meager knowledge of this species, we studied one population in the Karchat Hills, western Sind, Pakistan, from September 6 to October 3, 1972.

The Kirthar Range borders the Indus plain along its southwestern margin. Near the southern tip of this range, at 25° 50' N, 67° 40' E, are the Karchat Hills, an isolated massif some 20 km in length and 6 km in width. The hills consist of a central convex plateau, 1030 m above sea level at the highest point, whose edges drop 300 m or

more to the plains, either as steep slopes or abruptly as rugged scarps. A maze of deeply eroded ravines dissects the massif, and in several places a section of the plateau has slumped to form a wide valley with an extremely uneven floor of limestone blocks and rock detritus. Since the area lies in a desert zone, with an average annual rainfall of less than 25 cm, vegetation is sparse. *Acacia senegal*, the dominant tree, grows thinly on the slopes, as do such spiny shrubs as *Zizyphus* and *Capparis*. Most of the ground is bare, no more than about 5 % of it being covered with *Cenchrus*, *Dichanthium*, *Cymbopogon* and other bunch grasses which grow wherever there is a little soil among the rocks. In general, the hills look somber and desolate, especially when the sun sears the slopes (the average daily maximum temperature during our visit was 39.5° C with a range of 36 to 43° C), and winds whip dust across the barren expanses.

We confined our observations largely to the southeastern quarter of the hills. Roughly 150 wild goats frequented that sector, about a third of the estimated total population in the area. Although the Karchat Hills are part of a wildlife sanctuary, some illegal shooting occurs with the result that the wild goats remain shy, often fleeing a long way as soon as they note a person on foot. Consequently we observed animals from a distance of several hundred meters with 20-power scopes, either by scanning the slopes from the plains or by hiding on top of a cliff. The latter method enabled us to watch herds as they left the cliffs at dawn to forage on the plateau until they moved from sight into ravines, usually between 0900 and 1000 hours, to spend the heat of day in the shade of trees and shallow caves. We observed wild goats for a total of 77 hours.

Description of animals

Detailed descriptions of the wild goat can be found in LYDEKKER (1900), ROBERTS (1967) and other sources. We limit ourselves to mentioning mainly those characters which we used to distinguish the sexes and age classes.

Females and young: Adult females are light brown in color except for a white abdomen, white insides of the legs, grayish face, black tail, dark chest patch, and a stripe of gray above and below each carpal joint. Their slender, curved horns are 20 to 30 cm long. WAHBY (1931) found that one female weighed 30 kg. Yearling females are somewhat smaller than adults both in size and horn length. The young, which were an estimated 6 to 7 months old at the time of our study, still followed their mothers closely. Although similar in color to females, they are much smaller and their horns are mere spikes some 12 cm in length.

Males: Yearling males, 1½ years old in September, look much like adult females, except that they are smaller and their horns are more massive and longer, some 30 to 40 cm in length. Class I males, 2½ years old, are larger than yearlings and their laterally compressed horns tend to be 40 to 50 cm long, sweeping conspicuously up and back in the typical scimitar shape of adults. Males of this class have a wispy beard, in contrast to yearling males and females which lack one. Class II males, aged 3½ years, are about as large as adult females. They have a prominent beard and a black flank stripe separating the buff side from the white abdomen. Horn length is roughly 50 to 60 cm, although much individual variation may exist among animals of an age group. Class III males, considered at 4½ years of age to be young adults, are larger than females. Some animals have a faint vertical slash of black on the shoulder. The horns may be 75 cm long and have a conspicuous knob or two along the anterior keel. Most class IV males were estimated to be 5½ and a few 6½ years old. The animals are twice as large as females and the color of their

pelage during the rut differs markedly from that of young males. The brown has been replaced by grayish white along neck and back. The face is dark, as is the ventral part of the neck. A broad dark collar encircles the shoulders. The front of the forelegs is black, except for the white knees, and a prominent flank stripe merges into a dark line along the anterior edge of the hindlegs. A short crest of dark hair runs down the spine. The horns are over 75 cm long. Class V males are fully adult, at least 6½ years old. One seven-year-old male weighed 90 kg (WAHBY, 1931). The brown portions of the pelage have now turned wholly gray, a striking silvery gray which makes the animal visible at a great distance. The horns may be up to 133 cm long (LYDEKKER 1900).

Population structure and herd dynamics

We classified 828 wild goats according to age class and sex, some several times in the course of the study. Only when it was possible to classify every member of a herd were the data used in our calculations. The composition of the population was as follows: class V male — 8.2 %, class IV male — 11.1 %, class III male — 5.7 %, class II male — 4.5 %, class I male — 6.0 %, yearling male — 8.2 %, adult female — 31.1 %, yearling female — 11.3 %, and young — 13.9 %. Males of classes I to V appear to outnumber adult females by a ratio of 1.1 to 1, but our sample may be slightly biased in favor of males because the inconspicuously colored females are readily overlooked when a herd is scattered. There are fewer yearling males than yearling females by a ratio of .7 to 1, a difference from the expected 1:1 ratio for which we have no explanation. Although yearling females took part in the rut, a visit to the Karchat Hills in March, 1973, showed that most were neither pregnant nor had young at heel. Thus, females usually give birth first at the age of 3 years in this particular population under prevailing conditions. Single young and twins are the rule but triplets also have been reported (WAHBY 1931). Reproduction and survival of young were good in 1971, as the figure of 62 yearlings to 100 adult females indicates, but in 1972 they were poor, there being only 44 young to 100 adult females.

Adult males may separate from the females for part of the year, roaming alone or in male herds (DANFORD 1875). ROBERTS (1967) mentioned male herds with 8 or 9 members, and one of us saw a herd of about 60 males in northeastern Iran in the month of June. According to the villagers near the Karchat Hills, the males joined the females around mid-August. By the time we arrived, most male herds had broken up. Only two male herds with 5 members and 6 herds with 2 members were observed during the study. In addition, a few solitary class IV and V males wandered through the hills, often standing motionless on some pinnacle as if looking for a herd. One such male, recognizable by a broken horn, was seen alone on September 7 and with herds on several occasions from September 14 onward. After the termination of the rut, probably in late October, the males did not separate immediately from the females, for large herds containing adults of both sexes were seen in March, 1973.

The number of animals in 66 herds was counted. Twenty four herds contained 2 to 10 individuals, 13 contained 11 to 20 individuals, 10 contained 21 to 30 individuals, and 14 contained 31 to 40 individuals. Twelve herds with more than 40 members were also seen, but we were able to count only 5 of these precisely, containing 42, 68, 69, 75, and 99 animals, respectively. Average herd size was around 22. DANFORD (1875) and STOCKLEY (1928) also found that herds may comprise as many as a hundred animals.

The basic social unit consists of a female with her young and sometimes a yearling as well. Many small herds, those with fewer than 20 individuals, contained only females and subadults. Forty two percent of the small herds had no large males (classes IV and V) in them. Class V males in particular were absent from small herds, 63 % of such herds being without one. On the other hand, only one herd with more than 20 individuals lacked a class IV male and one had no class V male. The average number of class IV males in large herds was 3.1 (range 1 to 6) and class V males 2.3 (range 1 to 7). Table 1 shows several representative herd compositions.

Table 1
Compositions of representative wild goat herds

Males						Females			Total
V	IV	III	II	I	Yearl.	Adult	Yearl.	Young	
		1			1	4	2	2	10
1	2	1		1	2	6	1	4	18
2	3	2	1	5	4	8	1	2	28
5	6	2	1	2	3	7	2	3	31
2	5	3		2	2	13	5	5	37

A herd is not a cohesive social unit, for groups of animals may split from or join it repeatedly in the course of a day. During the morning, while feeding on the plateau, herd members may remain together for several hours, but at other times, particularly when foraging on cliffs, herds tend to break into small units.

Courtship behaviour

Rutting males exhibit several distinctive behaviour patterns. We quantified a number of these, recording them whenever they were observed. Occasionally several males displayed at the same time and it was then not always possible for us to note every action. In such a situation, the behaviour of only selected animals was recorded. Males typically repeated a display or presented a medley of displays to females, behaviour termed a display sequence in this report to distinguish it from individual patterns.

Description of displays: The behaviour patterns of rutting males can be divided into several categories: 1. those which mainly involve spreading odor, 2. those which emphasize physical attributes, 3. those which are used to test the estrous state of the female, and 4. those which are displayed when actively courting.

1. The tail of a male normally hangs down, but during the rut it may be straight up or folded over against the rump, positions which presumably help to dissipate odor from the tail glands. Tail positions change constantly with the activities of a male. One animal, for example, foraged with his tail hanging limply. When a female came near him, he raised his tail horizontally, and then, when he approached her, vertically. Finally he displayed to her with his tail bent over the rump. Tail positions of a sample of males were noted at the same time as we classified the animals, and, as Table 2 indicates, many males had their tails raised.

On 4 occasions a male lowered his rump and with unsheathed penis urinated against the back of his forelegs. A more common gesture, observed 61 times, was for a male to draw in his rump and turn his muzzle toward his bared penis. Some-

Table 2
Tail positions of males

	Age Class					Yearl.
	V	IV	III	II	I	
Sample size	76	101	55	36	33	22
Tail above horizontal	83 %	68 %	44 %	22 %	12 %	23 %
Tail horizontal	9 %	15 %	20 %	3 %	9 %	18 %
Tail below horizontal	8 %	17 %	36 %	75 %	79 %	59 %

times he nuzzled the penis, and at other times he inserted it once or twice into his mouth. On a few occasions he doused his face with squirts of urine. An Alpine ibex (*Capra ibex*) may ejaculate after nuzzling his penis (AESCHBACHER, in press), but the wild goat was not observed to do this. A male may interrupt a courtship to nuzzle his penis or he may show such behaviour in no particular context.

2. Males may use various lateral displays while following or remaining near a female. In one, the head-up, the male stands behind, beside, or occasionally on a ledge above the female, holding himself erect with his muzzle raised above the horizontal. In another display, the head-down, the male follows the female with his head lowered, muzzle pointing at the ground or tucked close to the neck, and with his back conspicuously humped. His steps are slow and stiff, and the long hairs along the back of his neck and shoulders bristle. The tail is raised as in the head-up. We saw the head-down only 6 times, given by class IV and V males. However, males sometimes trailed females with their neck more forward than usual and their chin pulled in, a posture which may represent a head-down of low intensity. A third display seems to contain components of both the head-up and head-down: the male stands by the female stiffly erect but with his chin tucked in. Males present these lateral displays not only during courtship but also during dominance interactions with others of their sex. One male may at such times display broadside to another or both may display mutually. The displays appear to be a means of showing off, of trying to impress another animal, whether it be male or female.

3. After approaching a female either in a normal posture or in a lowstretch (see below), a male frequently sniffs or nuzzles her perineal area. More often than not the female responds to the gesture by moving away. On 4 occasions she jerked her horns at the male or poked him in the body. At other times, however, she squats and urinates after being sniffed. Occasionally the male holds his muzzle into the stream of urine, but usually he waits until she finishes before he sniffs the ground. Then he raises his muzzle high with his lip curled up (*flehmen*), sometimes standing motionless in that position for at least 10 seconds before following the female or ignoring her while testing perhaps another female nearby. When a male sees a female urinate, he may come from 30 m or more away to check the site. Lip-curling is also observed after a male has investigated some spot where presumably an animal has urinated earlier, and after he has nuzzled his penis. The incidence of urinating in response to being sniffed increased among females as the rut progressed, rising from 18 % during the first half of the study to 38 % during the second half.

SHANK (1972) speculated that much of the courtship in male domestic goats (*Capra hircus*) is actually "urine-soliciting behaviour". This hypotheses can be checked by noting what behaviour of males elicits urinating in females. Wild goat females were observed to urinate 65 times during interactions with males, 34 % of the time when the male merely approached or followed, 43 % after being sniffed, and 23 % after

the male had performed a lowstretch, twist, or kick, sometimes in combination with a sniff. These figures show that female wild goats tended to urinate not in response to vigorous courtship displays but to rather casual gestures such as an approach or sniff. It seems unlikely that male wild goats would have evolved elaborate displays to stimulate a female to urinate, when, in fact, better results are achieved by simple gestures.

4. A male may display in several ways to a female which is in estrus or close to it. Holding his neck low and horizontally and straining his muzzle forward, the male approaches the female in a lowstretch (*Streckhaltung*). His body is sometimes lowered into a slight crouch as he walks or trots toward the female, usually from behind. Another display, the twist (*Kopfdrehen*), consists of rotating the head rapidly some 45° to 90° so that the horns are turned away from the female. A male may twist to a female from the front or side, but usually he is behind her, his shoulder almost level with her thigh. Sometimes he shoves her with his chest as he twists. A courting male also kicks (*Laufschlag*), raising a foreleg stiffly some 5 to 25 cm off the ground, seldom, however, touching the female in the process. On a few occasions, the upward leg movement of the kick was extended into a mounting attempt, suggesting, as SHANK (1972) pointed out, a close relationship between the two gestures. Sometime a male merely jerks a foreleg without lifting it, apparently an intention movement to kick which we did not quantify. The twist is the most common of the three displays, followed by the kick and lowstretch (Table 3). These displays are often accompanied by a flicking of the tongue and a wickering or grunting sound. We were unable to quantify these gestures because the animals were usually too far away.

Display frequencies changed during the rut. The lowstretch was the main display early in September, but it had become rare by the end of the month (Table 3). We cannot explain this change except to suggest that as the rut becomes more intense the gentle lowstretch is discarded in favor of more assertive displays. The number of twists and kicks per hour of observation show statistically significant increases from week to week ($X^2 = 47.9$, d.f. = 3, $p < 0.001$), as do number of sequences per hour of observation ($X^2 = 8.0$, d.f. = 3, $p < 0.05$). When statistically comparing the distribution of the three displays within single weeks, it was found that there were significantly more lowstretches than twists and kicks during the first week of observation. In fact, all figures for each week are significantly different except the number of twists and kicks during the first week. A *t* test on the standard errors of differences between means of displays per sequence (Table 3) shows that all are significantly different ($p < 0.001$) from each other except for the third and fourth weeks.

Although a courting male may limit himself to only one display, he often presents a sequence of them, either several of the same ones or a combination of the three.

Table 3

Display frequencies at various times of the rut

	Sept. 6-12	Sept. 13-19	Sept. 20-26	Sept. 27- Oct. 3
No. display sequences observed	7	44	95	100
No. sequences per hour of obs.	0.4	1.6	4.1	9.7
No. lowstretches	6 (86 %)	40 (51 %)	108 (17 %)	40 (5 %)
No. twists	1 (14 %)	31 (39 %)	376 (59 %)	487 (62 %)
No. kicks	0	8 (10 %)	157 (24 %)	265 (33 %)
Average no. displays per sequence	1.0 ± 0.0	1.8 ± 0.3	6.7 ± 1.1	7.9 ± 0.9

The combinations tend to follow a certain pattern. A lowstretch, if given, almost always precedes a twist, and, in fact, the two may be performed in one continuous motion. The twist and kick are usually executed simultaneously, whereas it is rare for a kick to occur during or after a lowstretch.

Males display more often and with greater vigor as the rut proceeds. They seldom displayed in early September, and, when they did, they limited themselves to a brief lowstretch or twist. On September 18 and 19, the rut suddenly intensified and probably reached a peak in early October. During that period, males displayed in long sequences, an average of some 7 to 8 displays per sequence with as many as 75 following each other in rapid succession. The average number of displays per sequence during the height of the rut as given in Table 3 represents a minimum for courting animals often moved from our sight. AESCHBACHER (in press) has shown for ibex that the number of displays in a sequence increases as the female approaches full estrus.

Occasionally a male remains some 10 to 20 m from an estrous female, moving and halting whenever she does, but usually he tends her closely, often with his head almost touching her rump. Now and then he may jerk his head down, as if to make her move. If she runs, he pursues, sometimes twisting behind her as they race in and out of ravines, around trees, and along ledges. After a run that may last a few seconds to several minutes the female halts and the male displays again, not in the restrained fashion of the early rut but with vigorous and jerky movements that may culminate in a mounting attempt. A female quite commonly repulses the male, presenting her horns to him or butting him in the head or neck, behaviour which we recorded 18 times. She may also back into a rocky niche or retreat backwards along a narrow ledge, thereby deterring the male. A receptive female stands or walks slowly with her back slightly humped and her tail held limply horizontal; she may also wiggle her tail rapidly back and forth. A condensed excerpt from our field notes describes the climax of a courtship:

The class V male twists and kicks and twists twice more as he stands beside the female. Gently he licks her neck. She takes a step forward. Twisting and rearing up with the same movement, he mounts her briefly. He dismounts and twists twice. The female rubs her face on his. He mounts again, gets off, twists vigorously, and mounts once more, just for a second or two. Then, standing parallel to the female, he twists and kicks. She nuzzles his face and neck and he reciprocates. Stepping back, he twists and kicks behind her, moves up beside her again, and they mutually nuzzle each other's face. He mounts once briefly and twists twice, always with much flicking of the tongue. Between displays he often has his tongue sticking out between his lips. The female licks his neck and face. He mounts her and she rubs her face against his. Twice he twists beside her. After another cursory mounting, he stands by her, his penis unsheathed, and twists three times. A class III male walks up, but, when the adult turns toward him, he scampers away. Slowly, walking side by side, the courting pair disappears from view into a ravine after having been in sight 15 minutes.

Mutual nuzzling and licking, as described in this example, were observed only at the height of courtship, except once when two class IV males behaved briefly in that manner.

The lowstretch, twist, and kick and associated gestures are with rare exception displayed only by males toward females, a situation different from that found in various sheep in which males commonly use these patterns also during agonistic encounters among themselves (GEIST 1971). However, on 4 occasions a wild goat male displayed courtship patterns to another male: one class V male kicked at another 3 times while sparring with him, a class IV male flicked his tongue and kicked at a reclining class IV male and took his rest site after he moved, a class IV male interrupted his courtship to flick his tongue and twist at a nearby class III male, and a class V male also behaved like that toward a class IV male under similar circumstances. In each case a dominant individual treated a subordinate one as

he would a female. SHANK (1972) found that feral domestic goat males may direct courtship patterns at other males after dominance fights, situations similar to those in which we observed the behavior.

Age differences in display frequencies: Males of all ages participated in the rut, but there were great differences in the amount of displaying by the various age classes. Few class II, I and yearling males had their tails raised above the horizontal, whereas almost half of the class III males and most of the class IV and V males had their tails in that position (Table 2).

Class IV and V males displayed most courtship patterns proportionately at least twice as often as would be expected from their number in the population (Table 4). These two classes were equally active in marking themselves with urine and sniffing females, but in actual courting and mounting the class V males were the main participants. Of the 24 mountings observed, one by a class V male appeared to have been successful. Class III males displayed relatively little, although they often hovered around courting pairs, and young males, those 3½ years or less old, seldom interacted with females in part because they were often chased away by older animals.

Table 4

Frequency of occurrence (in percent) of some courtship patterns
in the various male age classes

Pattern	Total No. Obs.	Age Class					
		V	IV	III	II	I	Yearl.
Percent males in age class		19	25	13	10	14	19
Urinating on forelegs	4	75.0	25.0	—	—	—	—
Touching penis with mouth	61	36.1	55.7	4.9	1.6	1.6	—
Sniffing vulva	105	32.3	48.6	11.4	2.9	2.9	1.9
Lipcurling	82	46.3	43.9	6.1	1.2	2.4	—
Lowstretching	194	50.0	43.3	3.6	1.5	.5	1.0
Twisting	895	48.9	39.2	8.4	.4	2.2	.8
Kicking	430	53.3	34.2	9.5	—	1.6	1.4
Mounting	24	66.6	12.5	4.2	—	4.2	12.5

During the few times when young males did attempt to court, display sequences were brief, limited to fewer than 8 patterns (average 3.0). Class III males behaved similarly except that an animal courted intensively on two occasions, displaying 21 and 41 patterns, respectively. With males mating little before the age of 5½ years and seldom living longer than 10 years, as revealed by growth rings on horns found in the field and collected by trophy hunters, they have at most 4 rutting seasons during which to contribute their genes to the population.

Dominance among males

Although there may be many males in a herd, these are quite tolerant of each other and aggression is uncommon except during competition for an estrous female. Class IV and V males tend to congregate within a herd, sometimes as many as 10 together, sniffing and briefly following any passing female, lip-curling side by side in response to the same urine, and otherwise behaving amicably. If several females are in estrus, each will be appropriated by a large male, and we have seen three

Table 5

Frequency of aggression (jerking, lunging, chasing, and butting only)
among age classes of males

Aggressor	Recipient						Total No. Aggressions
	V	IV	III	II	I	Yearl.	
V	12	43	33	5	4	6	103
IV		8	7	2	2	1	20
III			1	0	2	1	4
II, I, Yearl.						1	1

couples near each other without strife. However, if a male is courting a female, he becomes intolerant of other males that evince interest in her, and he attempts to chase them away. In such a situation, competition for the female could be severe unless established priorities exist. That there are priorities was intimated earlier when it was noted that class IV and V males do most courting. Dominance, and with it the right to an estrous female, can be established in two ways: 1. by displaying certain status symbols to which another animal responds without there being a need for a test of strength, and 2. actual combat to determine the strongest animal.

Males in the various age classes differ markedly in size, pelage color, and horn length. These physical characters act as status symbols in that a smaller male generally avoids conflict with a larger one. It was, for instance, common for a young male to leave a path casually or begin to graze intensively at the approach of an adult. Several males are usually attracted to an estrous female but the largest one appropriates her without being challenged by his smaller rivals. He prevents them from venturing close to the female with various aggressive gestures including a jerk of the head during which the horns are pointed at the opponent, a lunge, a chase, sometimes for 30 m or more, and actual contact in the form of a butt in the body. Such butts may be violent. For example, a class IV male had mounted a female when a class V male rushed up and butted him so hard in the neck that he almost fell. We recorded 128 aggressions of this kind (Table 5). Males usually threatened animals smaller than themselves, with class V males being particularly active in this respect. Size and other differences are often apparent even among two males of the same age class, and the smaller of the two usually retreats in a competitive situation. An example from our field notes describes the ways in which males displace each other around a female:

A class III male twists and kicks once behind a female. Another and somewhat larger class III male trots up and cuts in front of the other, taking his place by the female without being challenged. Immediately afterwards a class IV male arrives and lunges at the larger of the class III males so suddenly that the latter has barely time to turn around and catch the blow with his horns. The class IV male backs off a meter, then clashes once more with his opponent before following the female. The two class III males, joined by a third, trail behind. A class V male appears, jerks his head at the class IV male, who hastily steps aside, and takes his position behind the female.

Occasionally a class V male attempts to prevent other males from approaching any females in his vicinity, regardless of whether they are in estrus. One such male tried to guard 3 females for several minutes from 6 inquisitive males, a task which kept him running almost continuously.

When two males are of about equal size, it may be conjectured that status symbols are not sufficiently distinctive to determine dominance without a test of strength by some form of horn clashing. Wild goats may clash while facing each other

and while standing side by side, sometimes following contact with a sparring match of pushing and head-twisting. One male may also rear on his hindlegs, standing sideways to the other animal, then twist his torso and tip his head toward the opponent, who lowers his horns ready to receive a blow, before lunging downward to clash. Occasionally both rear and clash either before or after their forelegs touch the ground again. Several clashes may follow in rapid succession. Clashing was infrequent among rutting wild goats, in contrast to various wild sheep which commonly use this form of combat (GEIST 1971; SCHALLER, MIRZA 1973). We tallied 48 clashing encounters, some involving repeated horn contacts, but only 6 of these occurred in direct competition over a female. Even males of similar size appeared to have a rank order, except in a few instances. On the basis of studying Alpine ibex, NIEVERGELT (1967) suggested that males establish rank by fighting before the rut with the result that there is little strife during the rut. This presupposes that all males recognize each other individually, an unlikely situation in a large population. However, relatively few class IV and V males were in our study area, and some of these no doubt had aggressive encounters in the past and remembered them. It is also probable that wild goats are much better at evaluating subtle differences in status symbols, both physical and behavioural, than we are, and two animals which to us appear similar may not look that way to a goat. Whatever the mechanism, although competition for estrous females may seem intense, actual combat is rare because males perform within the framework of a hierarchical system.

Discussion

Several members of the genus *Capra* have been studied in detail, and we shall compare some aspects of the courtship behaviour of Alpine ibex (STEINHAUF 1959; WALTHER 1961; NIEVERGELT 1967; AESCHBACHER, in press), Kashmir markhor, *Capra falconeri cashmiriensis* (SCHALLER, MIRZA 1971), and feral domestic goats of mixed breed (SHANK 1972) with that of wild goat. Since the wild goat is thought by some to be the sole progenitor of the domestic goat (ELLERMAN, MORRISON-SCOTT 1951), behavioural comparison between these forms are of special interest.

The adult males of wild species are often solitary or in male herds except during the rutting period. The domestic goats studied by SHANK (1972) showed no marked sexual segregation, probably because in that population some mating occurs all year. However, social organization can be influenced by environmental conditions, and feral goats living in a more severe climate than coastal British Columbia, where SHANK observed them, might show breeding and herding patterns similar to those found in other *Capra*. Otherwise the general rutting behaviour of the four kinds of *Capra* is similar. Several males are usually in a herd with the females and maintain a rank order with the largest individuals appropriating estrous females and deterring smaller males from doing so by using a variety of aggressive gestures from a horn threat to a chase and butt. Large males consequently do a disproportionate amount of courting, both in the number of interactions and number of displays per interaction. A courting male remains near an estrous female, displays to her, sometimes chases her, and may be either rebuffed with a poke of her horns or nuzzled by her as an indication of her receptivity. SHANK (1972) noted several instances of social disorder among courting domestic goats with several males indiscriminately chasing and mounting a female and fighting with each other regardless of rank. AESCHBACHER (in press) observed several ibex males displaying communally to a female, behaviour which resembles that described for domestic goats but at a low intensity.

Turning to individual courtship patterns, the behaviour of ibex, markhor, domestic goat, and wild goat is again alike, although slight differences exist in the execution of several displays. Rutting male goats may fold their tails over their rumps. Domestic goats differ from wild species in that both males and females often carry their tails raised horizontally or vertically even when not sexually active. Both domestic and wild forms nuzzle penises, insert penises into the mouth, and spray forelegs and heads with urine. A *Capra* male regardless of species also sniffs the perineal areas of females, stimulating the animals to urinate, then checks the urine before raising his muzzle with the lip curled up. Markhor, ibex, and wild goat males often wait until after the female has urinated before sniffing the fluid on the ground, in contrast to the domestic goat males studied by SHANK (1972) which usually let the females urinate directly into their mouths. Specific differences in the head movements of lip-curling males possibly exist. A wild goat male tends to keep his head motionless, whereas an ibex and markhor male may wave it from side to side, and in the latter species, also abruptly up and down.

Lowstretching, twisting, kicking, tongue-flicking, and wickering are probably found in all *Capra*, for not only do these patterns occur in the four kinds under discussion but also in the tur (*Capra caucasica*) according to STEINHAUF (1959) and WALTHER (1961). Wild goats execute the lowstretch rather quickly, and, on the whole, the display is not elaborate. A male ibex, on the other hand, may just stand by a female in a lowstretch. The lowstretch of markhor appears to be less cursory than that of wild goat but not as prolonged as that of ibex. Wild goat and markhor kick stiffly, the foreleg held straight, whereas ibex paw the air with the carpal hanging limply. SHANK (1972) noted that the domestic goats he observed kick stiffly but with the foreleg bent. We have seen domestic goats kick with a straight leg, indicating that breed or population differences may exist. These displays have not been studied quantitatively except in ibex and wild goat. Leaving out tongue-flicking and wickering, AESCHBACHER (in press) recorded 3786 displays among ibex of which 11 % were lowstretches, 45 % were twists, and 44 % were kicks. The comparable percentages for wild goat were 13, 59, and 28. Wild goats twisted more and kicked less than ibex, but these differences have possibly little significance because the ibex data were obtained from a small captive herd.

The various goats differ greatly in their use of lateral displays. The head-up of wild goat has also been described for domestic goat and markhor, but not for ibex. An erect posture with chin tucked in is found both in wild goat and markhor, but SHANK (1972) does not mention it for domestic goat. It is also absent from the repertoire of ibex, and in fact, WALTHER (1961) noted that ibex seem to lack all lateral displays. The headdown of wild goat has not been described for the three other kinds of goat, although a display resembling it occurs in tahr (*Hemitragus*), which are primitive caprids, as well as in some rupicaprids. For example, the mountain goat (*Oreamnos americanus*) may display itself broadside to an opponent while walking stiffly with back hunched and neck arched far down (GEIST 1965). The Nilgiri tahr (*Hemitragus hylocrius*) employs a similar posture (SCHALLER 1970).

Since most *Capra* and related genera have not been studied in detail, it is difficult to evaluate the similarities and differences in behaviour found among the four kinds of goat described here. Except for the head-down display, the behaviour of rutting markhor and wild goat is alike, more so even than that of wild goat and domestic goat. After at least 8500 years of domestication (REED 1959), during which social and environmental pressures on the animals have been quite different from those acting on wild forms, it is not surprising that the behaviour of domestic goats has changed somewhat from that found in their probable progenitors. Besides differences in the